SHORTER ARTICLES AND DISCUSSION

AN INTRINSIC DIFFICULTY FOR THE VARIABLE FORCE HYPOTHESIS OF CROSSING OVER

THE assumption of a "variable specific force," made by Goldschmidt,[1] may seem to account for the frequency of the crossovers occurring in a given simple case of linkage; but when this explanation is extended to the results which such crossovers give when bred, it creates a difficulty of the same type and magnitude as the original problem of crossing over, for which, therefore, it is not a satisfactory solution.

Briefly put, the explanation advanced by Goldschmidt assumes that the genes are carried by the chromosomes, and that each gene is incorporated in its characteristic locus by virtue of a force residing in the chromosome and possessing properties specifically related to the properties of the genes of that locus. In the heterozygote Gg (see accompanying figure, line 1), the two forces F_G and F_g residing in the homologous chromosomes C and C′ possess not only a locus specificity but also an allelomorphic specificity corresponding to the allelomorphs G and g. When the chromosomes of the Gg heterozygote go into a resting stage, these forces F_G and F_g relax, so that the genes G and g become freed. When the chromosomes are reassembled preparatory to division these forces again come into play with the result that gene G is again incorporated into the chromosome in which F_G resides, while gene g is likewise reincorporated into the homologous chromosome characterized by the presence of F_g. In order that crossing over may occur, the allelomorphic specificities of forces F_G and F_g must, in the first place, be commensurable variables; *i. e.*, forces F_G and F_g must vary in that property which constitutes their essential difference, and in such a manner that when all the values of force F_G are represented by a characteristic frequency distribution and likewise all the values of F_g are represented by a second specific distribution, these two distributions will have a common base (see diagram, line 1). In the second place, these two distributions must overlap on the common base line so that a value chosen from the lower range of one may

[1] Dr. R. Goldschmidt, "Crossing over ohne Chiasmatypie?" *Genetics*, 2: 82–95.

be of the same magnitude as a value taken from the upper range of the allelomorphic distribution, though *the two forces thus chosen are,* of course, *no more identical than are two of Johannsen's beans which are of the same size but belong to different pure lines.* It is then assumed that in those cells in which the values of F_G and F_g are equal, the chromosome carrying F_G should incorporate gene g as frequently as gene G, and in those cells in which their normal order of magnitude is inverted, the crossover incorporation should occur more frequently, depending on the amount of inversion. Let us assume that in a given case this overlap is of such a per cent. that one per cent. of the gametes are crossovers (%1 of the diagram).

Now, in order to present the crux of the matter, let us proceed with the analysis of the behavior of the crossovers produced in the above experiment (see diagram, line 2). Let us mate a cross-

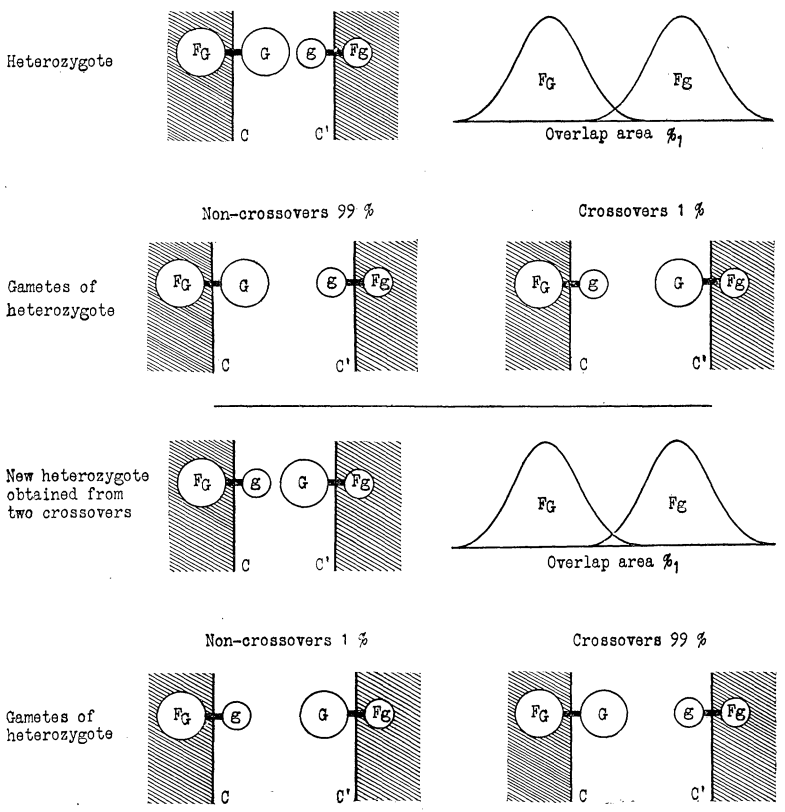

FIG. 1.

over individual in which gene G is held incorporated by force F_g with the converse crossover individual in which gene g is held incorporated by force F_G (see diagram, line 3). As soon as the chromosomes of the resulting heterozygote enter the proper resting stage the forces F_G and F_g relax, freeing the genes G and g. It must now be recalled that every value of force F_G is a member of a specific frequency distribution representing the entire behavior of F_G, and that any particular value of force F_G should give in succeeding generations the same result as every other value of F_G. Each value of F_G, whether chosen from the extreme upper range, the extreme lower range, or the mid-region, should give rise among its descendent cells to a series of variates which reproduce the original distribution F_G and no other. That is, the two distributions which describe the variates of F_G and of F_g in the cells of the new heterozygote, being specific, overlap in exactly the same fashion and to the same extent as did the distributions of the forces F_G and F_g in the original heterozygote (see diagram, line 3). Consequently, when the chromosomes are reassembled force F_G will, as before, incorporate gene G in 99 per cent. of cases and gene g in 1 per cent. of cases (see diagram, line 4). *But gene G entered the heterozygote as part of the chromosome possessing force F_g, hence the 99 per cent. of emerging offspring in which gene G is incorporated by the chromosome bearing F_G or gene g by the chromosome bearing F_G are crossovers.* As everyone acquainted with linkage knows, the crossovers given by the heterozygote from the mating of two crossovers are of the same frequency as in the original experiment. The intensities of coupling and of repulsion are *equal* and not complementary. Goldschmidt's machine which at the first revolution turned out a mere driblet of crossovers, should overwhelm the operator with a deluge of crossovers at the next turn of the crank. The whole explanation fails unless some added agency be devised to take over the duty which the specific allelomorphic forces abandon after the occurrence of crossing over.

The original problem was to secure the replacement of gene G in chromosome C by gene g, and at the same time the replacement of gene g in chromosome C′ by gene G. Having assumed the machinery of specific variable forces to accomplish this interchange, we find that the products of the interchange are not stable, and furthermore they give a result the opposite of that demanded by the well known facts of linkage. In order that

gene G should be stably related to its new position in chromosome C′ it must be held incorporated by force F_G and not by force F_g as is the case. Added on to the original problem of the interchange of the genes is now the second and equally imposing problem of the interchange of the forces subsequent to the interchange of the genes. An actual bodily interchange of the forces seems impossible in view of the assumptions we have had to make as to their nature and action. The transformations would then have to be accomplished by some transmutation *in situ*. It is evident that no internal autonomous change short of a complete and absolute mutation of force F_G in chromosome C into F_g and simultaneously of F_g in C′ into F_G would suffice. But we have no precedents for assuming such reciprocal mutations, and if we had, we could have sidetracked this whole machinery by applying this reciprocal transmutation idea to the genes and thereby solved the first problem in such a way that the second could not arise. Instead of localizing the cause of the reciprocal transformations of the forces in the forces themselves, one might transfer it to the genes; *i. e.*, one might endow the genes with the power of causing reciprocal transformations of the forces rather than empower the forces to transmutate of their own accord. While this form of the transmutation idea carries something of an air of plausibility, it can not be taken as more than an attempt at formal escape from the difficulty—a lifting of one's self by one's boot straps that makes more demand on credulity than, for example, one would in assuming crossing over offhand as a specific property of genes which needs, as support, only such formal explanation.

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ON THE PROBABLE ERROR OF MENDELIAN CLASS FREQUENCIES

AN old friend of geneticists who dislike excessive calculation has recently been attacked by Pearl,[1] viz., the familiar formula, $\sigma = \sqrt{npq}$ for the standard deviation of a Mendelian class frequency. He proposes to substitute a more refined but much more complicated method, originated by Pearson. In a Mendelian illustration he obtains a result which differs by over 40 per cent.

[1] Pearl, R., "The Probable Error of a Mendelian Class Frequency," AMERICAN NATURALIST, Vol. LI, pp. 144–156, 1917.